ADAPTATION FROM THE POINT OF VIEW OF THE PHYSIOLOGIST[1]

PROFESSOR ALBERT P. MATHEWS

THE UNIVERSITY OF CHICAGO

I FEEL much ashamed in having to expose my intellectual nakedness before the members of this society. When I came to this meeting I supposed that adaptation, or the fitness of organisms to their environments, was a physiological truism; that fishes were fitted by their structures and functions to a life in the water; that frogs were so constituted that they could live either on land or in water; and I was even so ignorant as to believe that many structures of a bird's body adapted it to flight. But it appears from the paper of one of my colleagues that in all of these things I was most woefully mistaken.

I feel some hesitation, also, in appearing before a society composed largely of American students of genetics, for I have no new and confusing terminology to propose; and owing to my ignorance of the language they speak and of the short-hand symbols sometimes employed, I am, perforce, compelled to speak in ordinary English which may be understood by any one; all of which, I fear, must invest all I have to say with an air of superficiality, or even of simplicity. I am besides a confirmed conservative in the matter of evolution, holding fast to the explanation of adaptation given by Darwin of natural selection of small variations; having little or no confidence that genes, unit characters, mutations, saltations, allelomorphs, determiners, inhibitors, dominants and recessives, genotyes and phenotyes, are anything more than ghosts, without substance; and looking always for simple explanations of a physical and chemical kind, capable of

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expression in ordinary language, of the apparent complexities of evolution. I avow myself as a physiologist to be a follower of Darwin, admiring his methods of careful experiment and observation, his long cogitations, and with confidence in the soundness of his judgment. There has been a tendency of recent years in certain quarters to belittle his work, to make fun of his conclusions, to deny that evolution has been a slow and steady continuous process, as the rocks show, and to assert that it has taken place by a hop, skip and a jump, and that it would have taken place anyway without natural selection. Physics and chemistry have attempted to express the physical world in terms of matter and energy, and many biologists are attempting to extend this method to the living world. While this is a necessary and admirable thing to do, it must not be forgotten that in doing so they are neglecting the main fact of life, consciousness, and that the phenomena of life can not be accounted for if this is neglected. It is obvious, too, that the physicist, with his present conception of matter and energy, is making as great a mistake in neglecting the psychical side of matter as the biologist would make if he neglected the physical side. For the psychical, like the physical, must be due to the properties of the atoms, or at least is associated always with them. For the atoms are the same in living and lifeless, their properties are inherent in them and can not be taken away and added to them as if they were wagons, which changed horses, as Du Bois Raymond has put it.

It is my opinion that physiology comes powerfully to the support of Darwin's conclusions; that it shows clearly that there are no such things as independently variable, unit characters; that a jump is a physiological impossibility; and that most so-called mutations are in reality reversions, as Darwin thought; and in this position physiology is, I believe, supported by paleontology.

But while accepting many of Darwin's conclusions, we must all admit that many phenomena are very hard

to understand on the basis of Darwin's explanations. Among these difficulties, most of which were recognized by Darwin, there are the phenomena of parallel evolution among different species and genera, which, though diverse, appear all to be moving forward in the same direction; the phenomena of steady, limited progress in one direction which point toward orthogenetic variation; the phenomena of the appearance of rudiments and their development until useful. It is exactly these difficulties upon which physiology throws some light; and it is of them that I particularly wish to speak.

In the evolution of animals two movements may be perceived: a spreading out and a progress; a diversification and a movement forward. The first movement is illustrated by the formation of many different species in one genus; or of many genera of the same type of animal; the second by the movement forward in the line of evolution of all these species. These two movements were not sharply distinguished by Darwin, but they have been more or less clearly recognized by several philosophers. It is this double movement which has given the animal kingdom the form of a branching tree instead of a single trunk. Darwin dealt mainly with the first of these movements, which gives rise to genera, species and varieties; which is shown by the diversification of animals and plants in domestication by human selection; and he explained it by the progressively better adaptation of forms to particular environments. He believed the second movement, the movement upward, was due to the same cause.

It is the second movement which has been so hard to explain and which has particularly puzzled the paleontologist; the successive series of dominating types on the earth's surface culminating in man; the progress steadily toward the goal of consciousness and intelligence.

The question which I wish to raise is whether these two movements, which are at right angles to each other, may not be due to the natural selection of two different kinds

of adaptations: first, adaptations of form and function to different kinds of environments; and second, the natural selection of the function of irritability, or, in other words, to the selection of adaptability, or the adaptation to changeableness of environment. Selection of the first kind of adaptations may have given rise to varieties, species, genera of the same type of animal, and have produced the spreading, or diversification; while selection of the second kind of adaptation may have produced the movement onward and upward of all animal forms.

These two kinds of adaptations do not always go together and selection of the one may outweigh the other. It is because selection to a specific environment sometimes is more important than selection of adaptations to changeableness, that not all organisms have progressed in the scale of evolution equally rapidly: but some have persisted in special environments with slight changes of structure for very long periods, or may even have retrogressed; while other forms, in which the second adaptation has been rigorously selected, have moved rapidly onward and upward, and show little adaptation to any special environment.

The question whether evolutionary progress is due to the selection of this second adaptation, that of adaptability, occurs very naturally to a physiologist, because, in the first place, the evolutionary development of consciousness and intelligênce appears to him to be one of the most important, if not the most characteristic movement in evolution; and in the second place, his point of view in considering evolution and adaptation is somewhat different from that of the zoologist or the paleontologist. To him the organism does not appear constituted of bones, skin, horns, or other structures, but to be constituted essentially of a number of mechanisms in activity, each mechanism having a definite function to perform. Evolution, for the physiologist, is not evolution of structure primarily, but evolution of function; and he natu-

rally expects to find that the adaptations of function have been of great importance in determining survival.

Of all the physiological properties of the original protoplasm upon which natural selection might be supposed to act, irritability, the most fundamental property of living matter, would seem the most probable point of attack; for irritability is that property of protoplasm in virtue of which it adjusts itself to its environment. It is the property of response; and since it is the environment which is acting as the judge of the excellence of the response and doing the selecting, it would seem that it must be upon this property that all organisms must be tested. It is, moreover, this property that Spencer has very acutely selected as the most fundamental characteristic of living organisms, namely, the power of continuous adjustment of internal to external conditions. It would seem probable that however well animals might be adapted to special environments by the action of natural selection, this particular property, or function, which has to do with the continuous adjustment of internal to external relations must have been throughout the whole course of evolution of predominant importance. And if there has been any unity in the progress; if the course of evolution has been at all in any single direction; and if the natural selection theory is true; it must be in the direction of the perfecting of this function.

I think this short statement will make it clear why the physiologist turns naturally to this fundamental quality, or property of living things, when he considers evolution and adaptation; for however organisms may vary in structure or other particulars, they all have irritability in common. Moreover, I think most physiologists will agree with me that this particular property has been too often neglected by most students of evolution, among whom physiologists have been unfortunately very rare.

Irritability shows itself in all cells by the power of internal change in response to an external change. In most cells of the body there is nothing especially adaptive

in the nature of many of these responses; but it is quite otherwise, if we consider the organisms as wholes. It is clear that all organisms have not only the power of reacting to an external change, but many of their reactions are adaptive to a surprising degree. This is indeed the very crux of the difference between living organisms and lifeless things. A lifeless thing can not adjust its internal to its external relations so that it can continue to exist in a changed environment. A crystal in a solution of its kind must dissolve, if the concentration is kept ever so little below saturation; a whole universe must pass away, if anywhere within it there is a persistent uncompensated difference of potential. With living things it is quite otherwise. They have the power of interposing resistances to the potential difference. All living things without exception have adaptive responses so that they are able to continue in existence even though their surroundings change in many different ways. They possess adaptability. Their responses due to their irritability are adaptive responses. The irritability of the organism as a whole is, then, above everything else characterized by power of adaptive response.

It is not difficult to imagine how this specialization of the general property of irritability arose. Some of the indefinite responses of the original organisms to environmental change protected the organism against the change. Organisms with such responses survived and their descendants had the property of a limited adaptive response to this particular change. From this crude beginning further progress was easy. The changes in the environment, though many, are not indefinite in number, and adaptations in the nature of direct responses easily arose and were perfected.

Adaptability, then, appears to the physiologist as the master word of evolution. And many facts also may be urged as confirming this conclusion. For example, one and all of the great physiological mechanisms of the body have a single purpose: to secure adaptability. Not to

adapt an organism to one environment, but to all environments, and thus to make it superior to all environments. Furthermore, the higher organisms are specially remarkable for the development of that master tissue of the body which is preeminently irritable and of which the main function is the adjustment of internal to external relations, the nervous system; and finally that the inference is sound may be concluded from the fact that it is by adaptability and by no other quality whatever that organisms may be arranged in the order of their evolutionary progress.

It is not at all surprising that adaptability should be the most important adaptation in nature, overpowering, except in special cases, and dominating all others. For there is but one certain thing in nature: namely uncertainty. The most constant feature of all environments, but particularly of land environments, has been their inconstancy. Changeableness is the chief characteristic of all environments, whatever their special characters may be. There are changes of light, temperature, climate, oxygen and carbon dioxide, moisture; changes due to the introduction of new species by migration upsetting nature's balance; changes in the food supply. Climates, flora and fauna change; change alone persists. Change is the essential thing. We may expect, therefore, if Darwin be correct in his conclusion that variation and natural selection account for evolution, that adaptation to changeableness must be the chief adaptation in nature, and more than all others, it must have determined the general course of evolution. This is found to be the case and the great physiological mechanisms of the body are designed, as already stated, to subserve this fundamental adaptation. Adaptability is that power which fits organisms to withstand the unexpected: the vicissitudes of life; special adaptations of form and color may contribute to the survival of animals; but the essential, or root, adaptation is to changeableness. By adaptation to all environments they become finally superior to all environments.

Superiority to environment, and not adaptation to it, is secured through the irritability of the organism considered as a whole.

The great mechanisms of the body which have this function are several. First, the heat-regulating mechanism, for by means of this organisms are rendered independent of the temperature of their environments. They can exist in the tropics or in the arctics and withstand the extremes of our own climate, while maintaining their activities. This is a complex mechanism consisting of insulating material in the skin; trophic nerves to the internal organs; a closed vascular system; a power of rapid oxidation; supra-renal capsules; pancreas; nervous coordination; sweat glands; evaporation of water in the lungs; temperature nerves. More than any other this mechanism enabled the mammals to conquer the reptiles and supplant them. The mammals became independent of the temperature of their environments. A mechanism not coming by jumps, but the rudiments found far down in the fishes and slowly evolved.

A second fundamental mechanism of great importance for the mammals in supplanting the reptiles and other animals probably was that concerned in immunity. Most of the toxins of poisonous reptiles are of a protein nature. The mammals have developed a mechanism, the details of which are still obscure, but which apparently consists in the conversion of these protein toxins into bodies which neutralize the toxins from which they are formed, that is, into antitoxins. We find, as a matter of fact, that at least many of the mammals are able apparently to make an anti-toxin out of any kind of a foreign protein. Besides this mechanism of defense, useful against bacteria, as well as against snakes, there is the primitive mode of phagocytosis and the chemical method of defense, which consists either in the prevention of absorption, or in the chemical neutralization of the poison by union with other substances. Thus the toxicity of phenols, benzoic acid and many alkaloids are neutralized. By this mechanism

mammals are rendered superior to the attacks of many of their enemies and to this extent rendered superior to their environments.

Third, there is the mechanism for rendering mammals tolerably independent of the moisture content of their environment, a mechanism most highly developed in the reptiles. A mechanism formed by the replacing of the wet skin of the amphibian by a dry or scaly skin; the perfecting of the kidneys to maintain osmotic pressure of the blood; the control of the sweat glands and loss of water by the intestines; the development of membranes non-permeable to salts, so that animals may sit in fresh water and not lose their salts. One of the most interesting parts of this mechanism is shown in the reptiles and birds, in the substitution of uric acid for urea in their excretions. By this improvement reptiles have secured almost complete independence of the water content of their environments. They make enough water in their own bodies to supply their small losses. This again is a mechanism of which we can trace the steady growth without a break from the invertebrates to man.

A fourth great mechanism makes mammals independent of barometric fluctuations and less dependent on a fixed atmosphere. By means of their blood loaded with hemoglobin carried in corpuscles lacking all oxygen-consuming power, they are able to live on lofty plateaus, or in deep valleys; and in the presence of much or little carbon dioxide.

The mechanisms having to do with reproduction and the caring for the young afterward have this same advantage of rendering the mammals independent of environment.

A sixth mechanism is the alimentary mechanism, most highly perfected in man. This has rendered him independent of any particular kind of food. He can make his body of any kind of plant or animal. He can make carbohydrate out of protein and many other things. He can live in any climate largely because of this mechanism.

Again a complex mechanism, consisting of teeth, of digestive glands tearing proteins and carbohydrates to pieces, so that he can build up his own proteins from any other kind, useless amino acids being converted into sugar and urea.

The last and by far the most important of these great mechanisms of adaptability is that which provides for every contingency; for the unexpected. It seems that nature, after elaborating these other mechanisms to meet particular vicissitudes, has lumped all other vicissitudes into one and made a means of meeting them all. One can not but be pleased by the apparent ingenuity of this solution. I refer to the nervous mechanism. It is obvious how this mechanism, by substituting choice for blind instinct, consciousness for unconsciousness, developing memory, so that one can profit by experience, and intelligent adaptation of means to ends, has provided finally for all possible contingencies of the future. She has spoken her last word. Adaptability, or superiority to environment, was the end so blindly sought; memory, consciousness, choice were the means, shall I say the means as blindly adopted?

To the physiologist, then, adaptability appears to be the touchstone with which nature has tested each kind of organism evolved; it has been the yard stick, with which she has measured each animal type; it has been the counterweight against which she has balanced each of her productions. However well adapted to a specific environment a type might be, did it lack ever so little of its possibilities in this direction, it was sooner or later relegated to the scrap heap. Some forms, to be sure, persisted in special environments, where they were protected from competition, as in Australia; or where the environment was fairly constant, as in the sea; or in special environments for which they were highly suited; but the whole trend of evolution, with these exceptions, may be summed up by the statement: the general course of evolution has been always from the beginning to the end, in the direc-

tion of increasing adaptability or increasing perfection of irritability. This law may be put by the side of the law for the evolution of universes: all spontaneous change is in the direction of increasing entropy.

It is not by form, by color, by increasing complexity or simplicity, that animals may be classified in the order of their evolutionary appearance. It is by this property of adaptability and this alone. At the summit is man; now consciously attempting to carry on what nature has been unconsciously attempting these millions of years, and to secure mastery of his environment. Below him are the other placental mammals of lower intelligence; beneath them the marsupials, less adaptable than the mammals, because of lower brain power; then the reptiles independent of water, but not of temperature; the amphibia, only partially independent of water, but not of temperature; the teleosts able to live in salt and fresh water; the selachians, most without osmotic control and limited to the sea; the arthropods living on land and sea, but dependent on temperature, food and climate, cramped by an external skeleton, and with the fatal defect of running the alimentary canal through the nervous system, so that for higher brain power, either a new nervous system or a new alimentary canal would be needed; lower still the molluscs and annelids, closely limited to their environments; and last the echinoderms and protozoa. No adaptation or power of the body has been so consistently attacked by natural selection as this; and it is this property which seems to have been the determining factor in the general course of evolution and to have determined the steady development of the psychic powers.

I come now to the second part of my subject, namely, correlation. By the first part I have attempted to show that the selection of variations in adaptability is responsible for at least a part of the steady progress in one direction of many kinds of animals; and explains that unity of progress which has been one of the main causes for assuming orthogenesis. In this second part of the

paper, I hope to show that the development of our knowledge of correlation removes some other difficulties which Darwin had to meet, and probably explains some other facts which have been urged as supporting orthogenesis.

Among the puzzles of evolution has been the steady growth of rudimentary structures which have apparently no function until they are considerably developed. I say *apparently* no function, for the physiologist has learned to be very cautious in saying that any part of the body is without function or use. A few years ago it was quite otherwise and it was supposed that various rudiments, like the appendix, the hypophysis, the pineal gland, the thymus and some other organs were without function; the surgeons were busy explaining how much better we were off without them; and the anti-Darwinian was fond of presenting these things as not consonant with the view of adaptation. At the present time the uselessness of these rudimentary structures is no longer affirmed. We must therefore be very cautious in supposing that any structure we see, no matter how insignificant it may appear, is without importance. Darwin himself felt the great fact of correlation, and his pangene theory was invented, in part, to account for these facts. He would be both astonished and delighted could he know how completely physiology has vindicated his appeal to correlation as the explanation of some difficulties.

Modern physiology has shown that the whole animal organism is correlated by means of internal secretions; that there is but one unit in the body, and that is the whole organism. By the work of Knowlton and Starling we now have the final proof of the correlation of the pancreas and muscles. The correlations between the hard and soft parts of the body are of still greater importance to the paleontologist, for it has been shown that the hard parts are not independently variable, but that they are dependent at every point upon the function of the soft, internal organs. Who would have dreamed that the character of the skin, the hair, the shape of the skull, the in-

telligence itself, the length of the limbs, or the speed of transformation of a tadpole into a frog would be dependent on the thyroid or thymus gland? That the minute parathyroids should be absolutely necessary to the life of an organism thousands of times their weight? Or that the development of the testes, the change of milk teeth to the permanent dentition, the growth of the bones of the extremities, should be dependent on the anterior lobe of that apparently useless rudiment, the hypophysis? Or that the secretion of milk and urine should depend on the posterior lobe of the same organ? Who had the temerity to suggest that the corpus luteum should be influencing the development of the mammary glands? Do we not see, indeed, that most of the characters of the body which have steadily developed from the fishes to man are secondary characters dependent on the anterior development of these ductless glands? Is this fact without significance to the paleontologist in helping him to understand the apparent steady progress in one direction, the appearance of orthogenesis? It will be asked, perhaps, what has caused the steady development of these glands. But the answer is not difficult. They are, in their turn, parts of the mechanism of adaptability which has been consistently selected in evolution. They are concerned not only in the growth of bone, but in the growth of the nervous system, the heat control of the body, the immunity mechanisms, the efficiency of muscles, and are in the chain of reproduction itself. These facts largely remove, in my opinion, the difficulties in understanding how rudimentary organs could be useful.

But not only do these facts remove these difficulties in the way of the selection theory, but they have a no less important bearing on the problem of heredity. They show that there can be no independently variable qualities in the animal body. The body is a unit, and I, at least, can imagine no part of it which can vary without influencing other parts. Correlations are everywhere. Pigment is often cited as a unit character, but how can it

be so? Pigment is itself the result of a long and complex series of changes. If a given cell produces no pigment it is perfectly certain that its other chemical processes are to some degree modified also, so that these other things vary also. If this cell is changed so that it produces no pigment, then since it is the logical result of a long series of changes in the developing organism, those changes must have been different in animals producing pigment and no pigment. But this means, since each process in the early stage of development influences a multitude of processes in the final change, that there must be a host of differences correlated with the pigment change. As a matter of fact, Darwin long ago pointed out that pigment production was apparently correlated with other factors; particularly with vital resistance, a fact repeatedly mentioned to the writer, also by Whitman as a result of his experiments in pigeon breeding. Darwin cites the case of the Virginia pigs of which only the black ones could eat a poisonous root without losing their hoofs; and Whitman told me that always birds deficient in pigment were also somewhat deficient in other characters and were weaker.

The essential unity of the organism is not only fatal to the whole theory of unit characters, but it is an insuperable objection to the theory that evolution has been by jumps. The organism is a finely adjusted mechanism of a very complex kind; it seems impossible to a physiologist that one can cause a sudden large change in any part of it and have it continue to function; it is as incredible as if one should remove one of the wheels of a watch, replace it by a larger one, and expect the watch to continue to run. Such a simple matter as the replacement of urea by uric acid as an excretion, a change which the reptiles introduced in their differentiation from the amphibia, a change which might conceivably be brought about by the dropping out of a uricolytic enzyme, could not take place suddenly. The kidneys and all other organs of the body would need to be adjusted to this change.

Finally correlation has greatly enhanced the value of the old idea of checks in development and shows most clearly that no organ of the body ever reaches its full potentialities. What comes out of an egg is but one of the infinite potentialities contained in it. Velocity of development, like every other chemical reaction, is equal to the affinity divided by the resistance. If resistances are increased, or if vitality, in other words chemical affinity, be reduced, the development must stop sooner than normal; and we have the phenomena of reversion. If, on the other hand, the reverse takes place, if vitality is increased or resistance reduced, we have variation in the direction of evolution. The development of nonviable monsters is at one extreme of this process. Ontogeny is like a runner, taking the first hurdles easily, but always with increasing difficulty, sometimes trippling at one, sometimes at another, but never reaching the end of his race.

In conclusion then: to the physiologist it appears that the best explanation of adaptation is that given by Darwin of natural selection of small variations; that the essential unity of the progress in evolution toward consciousness and intelligence has been due to the natural selection of the fundamental property of irritability, for it is in virtue of this property that adaptability of organisms has been increased. The recognition of this fact removes one of the difficulties in the way of Darwin's theory. And, second, physiology by the establishment of the physiological correlation of all parts of the body, hard and soft, interposes a final objection, in my opinion, to the whole theory of unit characters, of independent variability of characters, and to the theory of evolution in any other way than by a slow and gradual process, which shall give time to the readjustments of every part of the body necessitated by a change, however slight, in any part of it.